An Allozyme Electrophoretic Study of Populations of Spiders of the Genus *Corasoides* (Araneae: Stiphidiidae) from Australia and Papua New Guinea

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Allozyme electrophoresis was used to delineate the boundaries of the spider genus *Corasoides*, clarify the identity of *C. australis* Butler, 1929, and identify putative new species within the genus. Fixed gene differences, together with similarity and distance trees, showed that *C. australis* was widespread across much of southern Australia while eight new species were differentiated that had comparatively narrow distributions in Australia and Papua New Guinea. Wagner trees were used to show phylogenetic relationships between these species.

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KEYWORDS: Allozyme, *Corasoides*, electrophoresis

INTRODUCTION

The genus *Corasoides* has only one described species, *C. australis,* Butler, 1929, commonly known as the platform spider. *Corasoides australis* is a medium sized spider which digs a burrow from which it constructs a non-sticky, horizontal sheet web with a tangled maze of threads above. The spider runs on the upper surface of the sheet web (Main 1976). The genus appeared to be widespread and the presence of more than one species of *Corasoides* had been suspected for some time in Queensland (R. Raven, pers. comm.), in the south west of Western Australia (B.Y. Main, pers. comm.) and in Papua New Guinea (Main 1982). Allozyme electrophoresis is used here to clarify the genus and species since it is particularly suitable for systemic studies at the species and intra species levels (Avise 1975; Richardson *et al.* 1986; Quicke 1993), and has been used to delineate spider species by several previous workers (Pennington 1979; Lubin and Crozier 1985; Colgan and Gray 1992).

MATERIALS AND METHODS

Live spiders were collected in the field from populations across Australia and Papua New Guinea (Table 1) and kept in captivity until needed.

Locations consisted of single sites when specimens from those sites were of sufficient number and/or the site was geographically isolated from other sites and/or were distinctly different morphologically or behaviourally.

Populations 1, 2, 3, 4, 5, 6 and 25 were from rainforest habitats. The habitats of the remainder ranged from sclerophyll forest to arid scrubland. Populations 2 and 3 were sympatric but have distinctly different morphology (author's observations).

Electrophoretic methods generally followed those of Richardson, Baverstock and Adams (1986). Mostly muscle tissue from live specimens anaesthetised with carbon dioxide was used and the supernatants obtained were stored at –80° C. Cellulose acetate plates were used to run eighteen enzymes plus general protein giving a total of 21 loci (Table 2). There was

Table 1. Populations sampled (for distribution of material sampled see Fig. 1)

Popn #	Name	Location
1	Kuper	Kuper Ranges, Papua New Guinea
2	Largetown	Tabubil, Papua New Guinea
3	Smalltown	Tabubil, Papua New Guinea
4	Ambua	Tari, Papua New Guinea
5	Windsor	Windsor Tableland, Queensland
6	Terania*	Nightcap and Border Ranges National Parks, NSW
7	Fraser	Fraser Island, Queensland
8	Blackdown	Blackdown Tablelands, Queensland
9	Gibralter	Gibralter National Park, NSW
10	Hornsby	Hornsby, NSW
11	South Coast*	Sydney, NSW to Victorian border
12	Victoria*	Victoria – east coast to Little Desert
13	South Australia*	South Australia, other than Wilpena and Nullarbor
14	Wilpena	Wilpena Pound, South Australia
15	Nullarbor*	Yalata, South Australia to Eucla, Western Australia
16	Kalgoolie	Kalgoolie and Coolgardie areas, Western Australia
17	Stokes	Stokes Inlet and National Park, Western Australia
18	Stirling	Stirling Ranges, Western Australia
19	Yallingup	Yallingup, Western Australia
20	Nannup	Nannup, Western Australia
21	Glenforrest	Glennforrest National Park, Western Australia
22	Cervantes	Cervantes, Western Australia
23	Greenough	Greenough, Western Australia
24	Peron	Peron National Park and Shark Bay, Western Australia
25	Clyde	Clyde Mountain near Monga, NSW

*Pooled sites. Sites were pooled into locations of greater geographical size when specimens were scarce and they did not appear to differ morphologically or behaviourally and/or specimens were widely scattered and not discontinuous.

no variation detected in results between male/female or juvenile/adult.

All locations were tested for Hardy-Weinberg equilibrium for each locus to confirm the absence of multiple species within locations, particularly in locations consisting of pooled sites.

Data were analysed using the computer program "BIOSYS" version 1.7 (Swofford and Selander 1981). Phenograms (trees based on similarity between populations) were derived using the coeficients Nei's (1972) genetic similarity, Nei's (1972) genetic distance, and Rogers' (1972) genetic similarity. Although overall similarity may be a reflection of phylogenetic distance (Colless 1970), phenetics does not take into account convergence or parallelism so phylogenetic relationships were assessed using Wagner trees. Trees were either rooted at the midpoint of the longest path or by use of outgroup taxa. Since the family affiliation of *Corasoides* is uncertain, four outgroups were selected. The use of *Badumna insignis* Koch, 1872 (Desidae) and *Stiphidion facetum* Simon, 1902 (Stiphidiidae) acknowledge family affiliations put forward by Lethinen (1967) and Forster and Wilton (1973). The two pisaurids, *Inola subtilis* Davies, 1982 and *I. daviesae* Tio and Humphrey, 2010 were also included as outgroup taxa as they share many similarites with *Corasoides,* particularly in behaviour and web structure.

RESULTS AND DISCUSSION

Phengrams derived using Nei's genetic similarity, Nei's genetic distance and Rogers' similarity are given in Figs 2-4. Wagner distance trees are given in Figs 5, 6.

Over 98% of the 525 permutation pairs in the ingroup agree with Hardy-Weinberg equalibrium. None were significant using exact probability and of the few that deviate from Hardy-Weinberg equilibrium, none were from locations where sites were pooled. This confirms the absence of multiple species within the sampling locations.

All three phenograms recognise three major clusters: the Papua New Guinea populations (Kuper, Largetown, Smalltown and Ambua), the Australian rainforest populations (Terania, Windsor and Clyde), and Australian non-rainforest populations (Fraser, Peron, Blackdown, Hornsby, South Coast, Victoria, South Australia, Gibralter, Nullarbor, Wilpena, Kalgoorlie, Greenough, Stokes, Stirling, Yallingup, Cervantes, Nannup and Glen Forrest). Nei's distance and Rogers' similarity grouped the Papua New Guinea

a n d

Fig. 1. Map of sampling sites.

Australian rainforest populations together and Nei's genetic similarity grouped all the Australian populations together. Within the Australian rainforest populations Nei's genetic distance placed the Terania and Windsor populations closer genetically to each other than to the Clyde population, while Nei's similarity and Rogers' similarity placed the Windsor and Clyde populations closer together. All phenograms were in agreement with the internal arrangement of the grouped Papua New Guinea populations and the grouped south-western Western Australian populations and also with the separation of these south-western Western Australian populations from the rest of the Australian dry habitat populations.

Delineation of species boundaries

Within the Australian non-rainforest populations, all phenograms recognised the division between the populations from south-western Western Australia (Stokes, Stirling, Yallingup, Cervantes, Nannup and Glen Forrest) and the rest of the sampled Australian non-rainforest populations previously tentatively regarded as *C. australis* (Fraser, Peron, Blackdown, Hornsby, South Coast, Victoria, South Australia, Gibralter, Nullarbor, Wilpena, Kalgoorlie and Greenough) and agreed with each other in regard to the internal arrangement of these populations except in a few minor areas.

Table 2. Enzymes used in this study.

No.	Enzyme	Abbreviation	Loci
1	fumerate hydratase	FUM	1
2	glucosephosphate isomerase	GPI	1
3	triosephosphate isomerase	TPI	1
4	alkaline phoshatase	AP (ALK*)	1
5	malic enzyme	ME (MEN*)	1
6, 7	malate dehydrogenase	MDH	2
8	mannosephosphate isomerase	MPI	1
9	glyceraldehyde-3-phosphate dehydrogenase	GA-3-PDH (3GP*)	1
10	glucose-6-phoshate dehydrogenase	G-6-PDH (G6P*)	1
11	6-phosphogluconate dehydrogenase	6-PGDH (6PG*)	1
12	glycerol-3-phoshate dehydrogenase	GPD	1
13	isocitrate dehydrogenase	IDH	1
14	esterases	EST	1
15	phosphoglucomutase	PGM	1
16,17	adenylate kinase**	AK (AKI*)	2
18	fructose-1,6-diphosphatase	FDP	1
19	hexokinase	HK (HKI*)	1
20, 21	general proteins	GP (GPR*)	2

* These abbreviations appear in BIOSYS data where a three letter code is needed.
** Adenylate kinase and creatine kinase gave identical multiple bands despite inhibitor used in the latter gels.

Since the type locality of *C. australis* is included in the population of Victoria, I regard the populations of Fraser, Peron, Blackdown, Hornsby, South Coast, Victoria, South Australia, Gibralter, Nullarbor, Wilpena, Kalgoorlie and Greenough as belonging to *C. australis*. These populations were found to have Nei genetic similarities between them ranging from 0.84 -1.00. These figures are in agreement with Avise's (1975) figures (approximately 0.70-1.00 for conspecifics). Similarly, the populations of south-western Western Australia (Stokes, Stirling, Yallingup, Cervantes, Glenforrest and Nannup) have Nei genetic similarities of 0.87 - 0.99 between them so these populations should be considered conspecific. The Nei's genetic similaries between the populations of *C. australis* and those of south-western Western Australia was 0.69 -0.82. (mean 0.75). Although these figures could be said to indicate a genetic similarity compatible with conspecifics, in all cases they are lower than the interpopulation similarities within either group. In addition, the two groups are quite distinct morphologically and biologically (author's observations). Thus, I consider the above pooled south-western Western Australian populations (hereafter referred to as SWWA) to be a sister species to *C. australis.*

The seven remaining populations (Kuper, Largetown, Smalltown, Ambua, Windsor, Terania, Clyde) had 21 permutation pairs between them and had Nei genetic similarity estimates of 0.42-0.85. Sixteen of these similarity estimates indicate separate species status but five are within Avise's (1975) estimates for conspecific species (0.70-1.00) namely Ambua/Smalltown 0.77, Terania/Windsor 0.85, Terania/Clyde 0.83 and Clyde/Windsor 0.83. Kupper/Largetown is borderline. Smalltown/Ambua is a terminal pair on all trees so its borderline conspecific similarity estimate is understandable. The remaining three pairs with high similarity estimates would ordinarily indicate that Terania, Windsor and Clyde are conspecific. However, all three are eastern Australian rainforest inhabitants and although being morphologically distinct in rapidly evolving sexual characters, probably reflect the conservative retention of biochemical attributes in species in similar habitats which have mostly remained unchanged from their ancestral habitat. I thus regard each of the seven populations as having separate species status and they will be referred to here using their population name as a code for their respective species.

Nei's genetic distance measurements were 0-0.17 between conspecific populations (in agreement

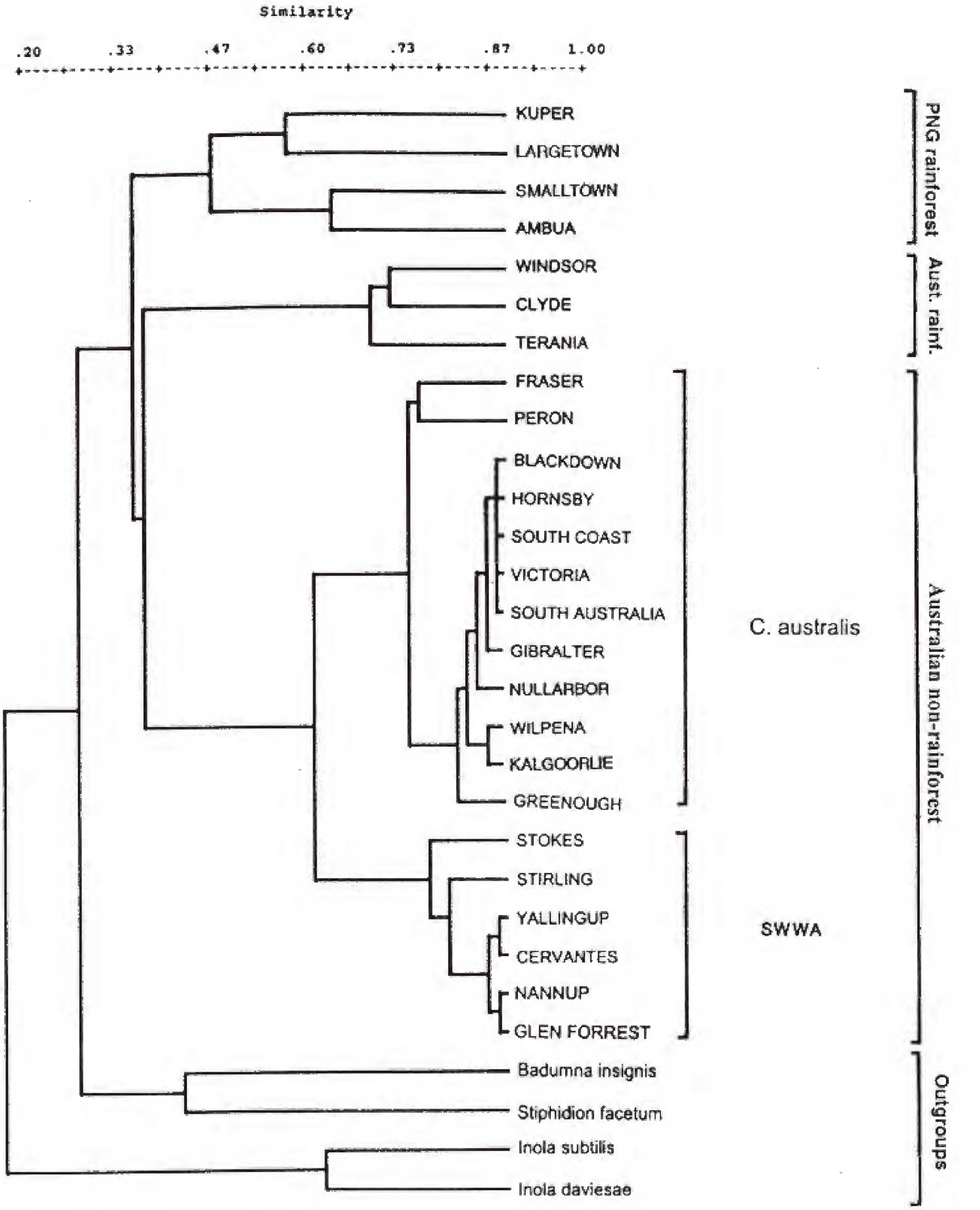

Fig. 2. Phenogram derived using Nei's genetic similarity coefficient of all populations of *Corasoides* sampled and using *Badumna insignis*, *Stiphidion facetum* and *Inola daviesae* as outgroups.

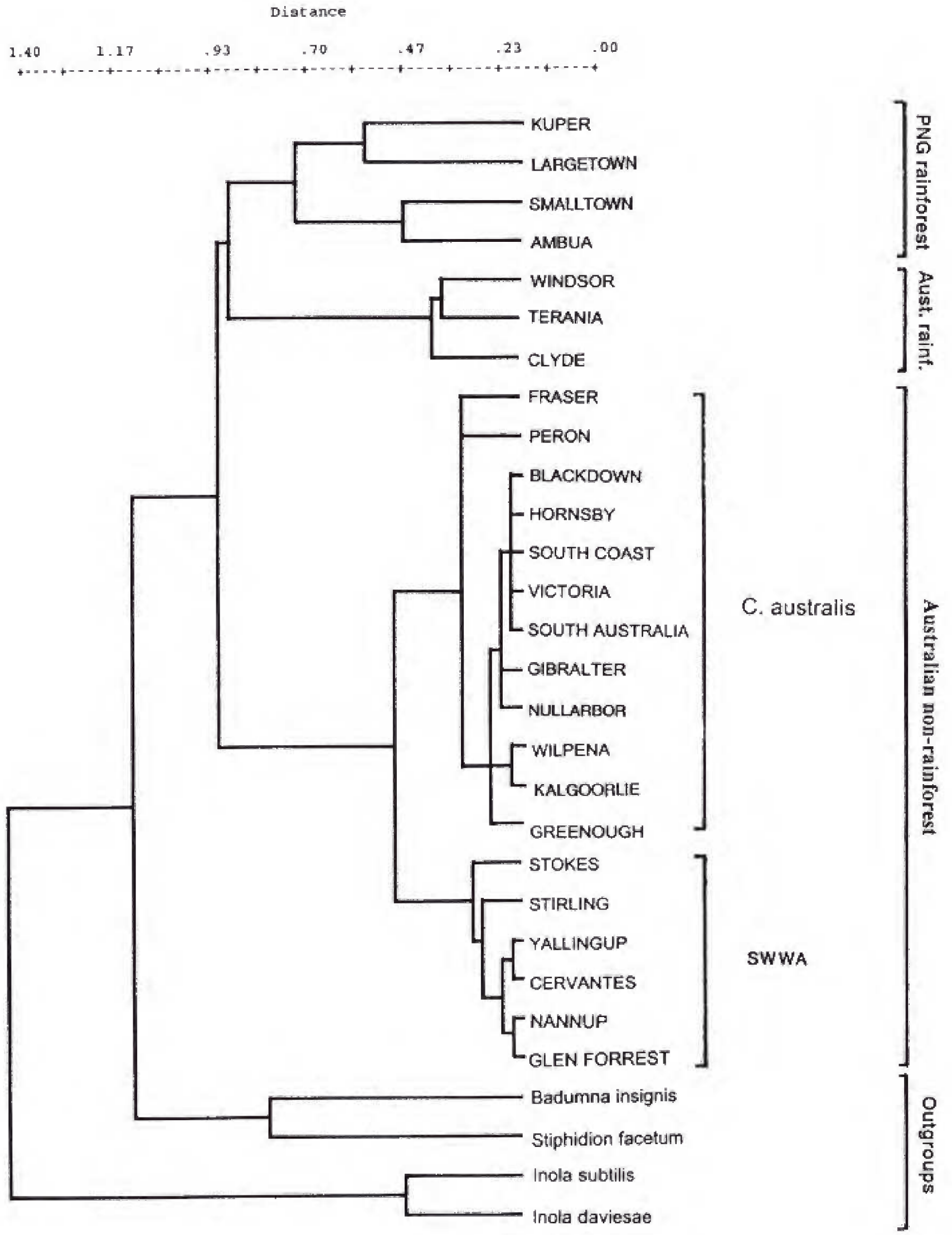

Fig. 3. Phenogram derived using Nei's genetic distance coefficient of all populations of *Corasoides* sampled and using *Badumna insignis*, *Stiphidion facetum*, *Inola subtilis* and *Inola daviesae* as outgroups.

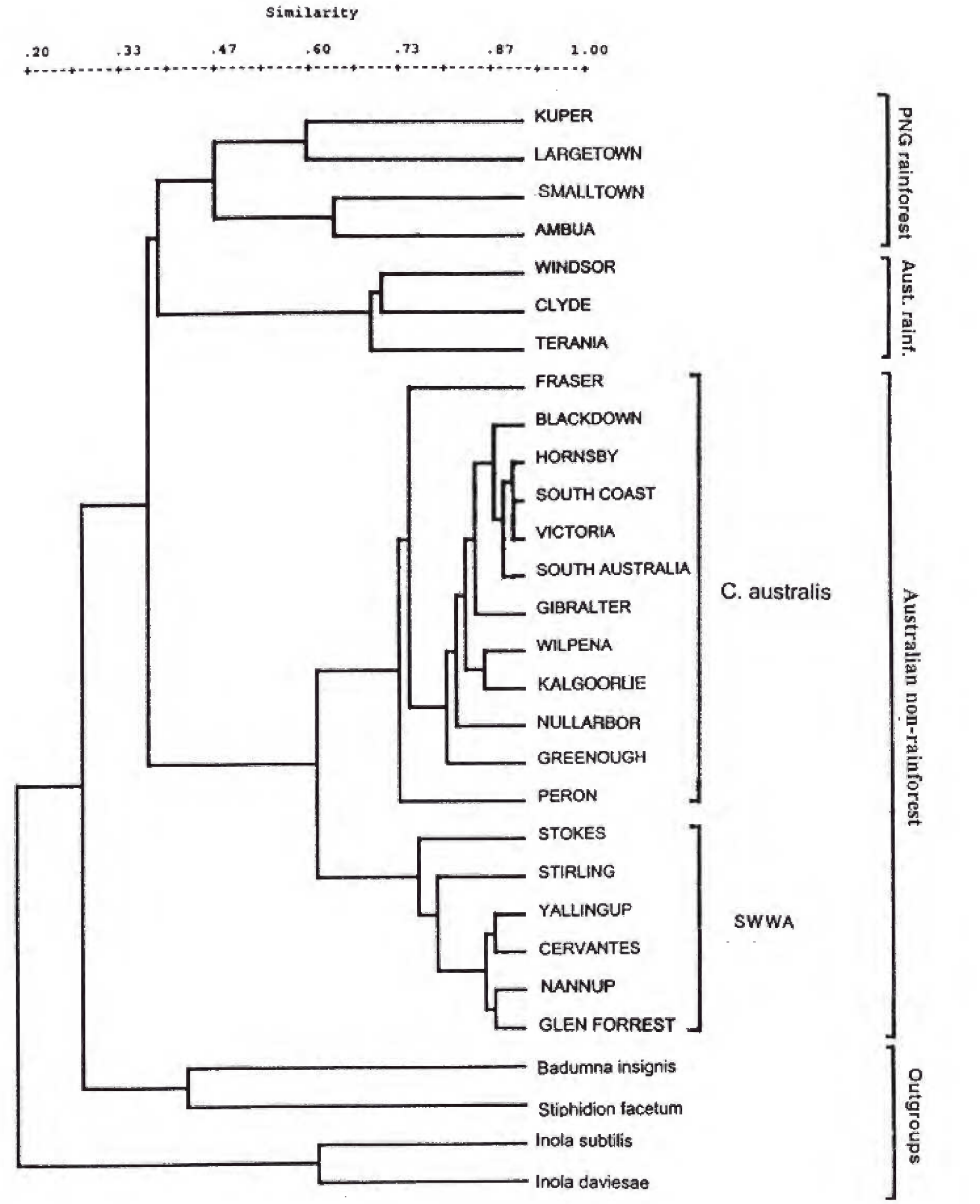

Fig. 4. Phenogram derived using Rogers' similarity coefficient of all populations of *Corasoides* sampled and using *Badumna insignis*, *Stiphidion facetum*, *Inola subtilis* and *Inola daviesae* as outgroups.

Table 3. Fixed differences between species

	Kupper	Large town	Small town	Ambua	Windsor	Terania	Clyde	SWW*A*
Kupper								
Largetown	(6)							
Smalltown	5	(5)						
Ambua	8	(3)	3					
Windsor	9	(10)	9	10				
Terania	7	(6)	8	10	2			
Clyde	9	(9)	8	9	3	3		
SWW*A*	8	(8)	4	6	7	4	3	
australis	5	(7)	4	7	7	5	3	1

Table 4. Percentages of fixed differences between species. Numerals in parentheses are disregarded due to small sample size.

	Kupper	Large town	Small town	Ambua	Windsor	Terania	Clyde	SWWA
Kupper								
Largetown	(29%)							
Smalltown	24%	(24%)						
Ambua	38%	(14%)	14%					
Windsor	43%	(49%)	43%	49%				
Terania	33%	(29%)	38%	49%	10%			
Clyde	43%	(43%)	38%	43%	14%	14%		
SWWA	38%	(23%)	19%	29%	33%	19%	14%	
australis	24%	(33%)	19%	33%	33%	24%	14%	5%

with the figures of Bruce and Ayala (1979) (approximately 0-0.25). Results between sister species within the ingroup were 0.17-0.34, slightly lower than those of Bruce and Ayala (1979) (0.20-0.65). Since Nei's genetic similarity and distance are associated these results are expected and the same explanations follow.

Interspecific fixed genetic differences

The number of fixed differences for all permutations between putative species is given in Table 3 with the percentage of fixed differences over 21 loci in Table 4. Results in parentheses must be considered with caution due to small sample size.

The highest number of fixed differences was ten. The highest numbers of fixed differences (scores of 8, 9 and 10) occurred, with but one exception, were between pairs consisting of an Australian and a Papua New Guinean species. The lowest numbers of fixed differences (scores of 1, 2 and 3), but for two exceptions, occurred between pairs of Australian species.

Baverstock, Watts and Cole (1977) indicate that 14% of loci with fixed differences are sufficient for consideration as separate species. Only two of these species permutations show fewer than 14% fixed differences.

However, caution is required when drawing conclusions from fixed differences obtained in this study because of the unequal number of sites sampled per species. Although seven populations were sampled for SWWA and eleven for *C. australis*, all other species were represented by only one or two locations. Polymorphism can be expected to rise with an increase in the number of isolated populations sampled and increased polymorphism leads, up to a point, to a lower number of fixed differences recorded. This would explain the low number of fixed differences between pooled populations of *C. australis* and SWWA. If alleles are not pooled

for SWWA and *C. australis* and single populations from them compared for fixed differences with other species, then the number of fixed differences increases dramatically so that the 14% level is reached for most permutations.

Intraspecific fixed genetic differences

(i) Within *C. australis*

There are two fixed differences involving Fraser, one (with MPI-1) separating it from all other populations except Blackdown and Peron, and another (with G6P-1) separating it from all other populations except Kalgoorlie, Greenough and Peron. There is one fixed difference for Peron (EST-1) separating it from all other populations except Fraser and Greenough but this must be considered with caution because of small sample size.

Similarly, a fixed difference observed in Wilpena (its single allele in MEN-1 shared only by Kalgoorlie and Blackdown) cannot be substantiated because of the small sample size of two. However, it should be noted that the Wilpena population appeared to be a small, sole, isolated population on the rim of the pound, a rather barren and hostile environment but the only one in the area which apparently had not been affected by cattle grazing. Morphologically the specimens were much smaller than most other members of the species but this could have been environmental, due to the harsh conditions. The habitat and size of specimens was similar for specimens from Kalgoorlie. Blackdown is not as harsh an environment and the area was protected from grazing within a State Forest and the Blackdown specimens were larger, intermediate in size to specimens from sclerophyll forest on the eastern Australian coast. Otherwise all three populations appear morphologically and behaviourally similar to other populations of *C. australis* (author's observations).

The two fixed differences involving Fraser are interesting in that they link Fraser with Greenough and Peron (and to a lesser extent, Kalgoorlie and Blackdown) indicating an apparent east-west link seen also for Peron EST-1.

Fixed differences within *C. australis* could be brought about by their clumped and extensive distributions over thousands of kilometres. This may lead to many locally inbred populations with the potential to become monomorphic for several different alleles. Summing the allelles present for *C. australis* it can be seen that this species is polymorphic for most enzymes, while other species are usually monomorphic. This greater detection of polymorphism is caused also by the imbalance in the sampling numbers; those monomorphic species usually having small sampling numbers so that there is a lower probability of detecting less common localised alleles.

(ii) Within SWWA

There were two fixed differences; one (with MEN-1) between the individuals of the population from Stirling Ranges and all other sampled populations of SWAW and the other (with GPR-2) between the samples from Stokes River National Park and all other sampled populations of SWWA.

The single fixed difference separating the Stirling Ranges population from other populations of SWWA may be just a regional adaptation. The Stirling Ranges, for instance, have a winter far colder than any other region in the distribution of SWWA. It remains to be seen whether populations from further down the slopes or from areas surrounding the Stirling Ranges carry this allozyme in the heterozygous state. (It is interesting that the only other specimens which carry the allozyme allele responsible for this fixed difference are *C. australis* from the Gibralter samples, the only other area sampled with a comparably cold winter). The population from Stokes River National Park is also geographically distant (300km) from the next closest sampled population. Unsampled populations within in this area could well be found to be polymorphic for the locus involved in the fixed difference with alleles common to the rest of the species.

(iii) Within Terania

One fixed difference was detected after calculation of Hardy-Weinberg heterozygote probabilities. In this study there are 88 population pair permutations for polymorphic loci. Of these pairs, twelve had a significant deficit of heterozygotes when calculated using chi-squared probabilities. Of these 12 pairs, five had fewer than five specimens in the sample and of the remainder all but one (Terania/GPD-1) were calculated as insignificant under exact probability. In this last case the sample was pooled, consisting of four specimens from Nightcap National Park and two specimens from Border Ranges National Park. These two locations are over 50 km apart and separated by the Tweed Valley. Since each of the sample sites was monomorphic for a different allele, there would be no deficiency of heterozygotes if the samples had not been pooled. However, there exists instead a single fixed difference between the two sampling sites. Overall, the results from fixed differences between sampled populations within *C. australis* is acceptable for conspecificity.

Delineation of genus

Similarity and distance measurements

There are 300 population pair permutations of *Corasoides* in this study. Of these, all but five (i.e. 2%), have a Nei genetic similarity estimate of at least 0.40. The lowest of these exceptions (0.365) is between Windsor and Wilpena (a small isolated population from which only two individuals were sampled). The other exceptions are between Windsor and four of the eastern Australian populations of *C. australis* (0.384, 0.388, 0.388 and 0.390) and between Largetowns and Kalgoorlie (0.393, another small population of *C. australis* with a sample number of two). With the exception of the above mentioned pairs, the estimates of Nei's gentic similarity are in agreement with the figures cited by Avise (1975) for congeneric species (0.40-0.70).

Distance measurements of populations within the ingroup of this study are often greater than those cited by Bruce and Ayala (1979) (0.20-0.65 for congeneric species). However, with only one exception (between Largetown and Windsor, 0.741), all distance measurements greater than 0.65 involve those populations belonging to the most highly derived species on the twigs of the trees.

The figures for both genetic similarity and genetic distance between the two outgroup species of *Inola* are similar to those between species of *Corasoides.*

Therefore, and with the support of morphological data (author's observations), all populations within the ingroup can be regarded as belonging to the one genus, i.e. *Corasoides*.

Phylogenetic analysis – Wagner trees

Both Wagner trees (Farris 1970) from BIOSYSIS (Figs 5, 6) support species status for the nine groups as indicated by the phenetic analysis.

Both Wagner trees, rooted either by midpoint of the longest branch or, by outgroups, also recognised monophyly of both the Papua New Guinea branch and the Australian branch and the further division of the Australian species into those from rainforest habitats and those from non-rainforest habitats. Within the Australian rainforest branch Clyde was the sister group to the other species. There were only minor differences of internal arrangement between the phenograms and the Wagner trees with respect to the Australian non-rainforest populations.

The phenetic trees either grouped together all the rainforest species, as opposed to the non-rainforest species, or failed to resolve them. This could be a reflection of a lack of sensitivity in phenetic methods to convergence and parallelism. Assuming that allozymes are not selectively neutral (Cook 1971, Lewontin 1974, McDonald 1983), natural selection of enzyme variation could be expected to be dependent upon components of habitat such as extremes and variation of temperature. Consequently, non cladistical methods would be expected to group together organisms with like adaptations to the same environment rather than considering the possibility of convergence and parallelism.

Summary of systematic implications

While the pheneticly derived trees are in conflict over the placement of the Australian rainforest group, both the phylogenetic Wagner trees placed it as the sister group to the non-rainforest group, thus dividing *Corasoides* into two monophyletic groups, the Austalian species and the Papua New Guinea species. However, the relevant branch distances in all trees are so short that little confidence can be placed in the position of this Australian rainforest branch from the results of these analyses. Nonetheless, all trees supported the existence of three major groups within *Corasoides*; the Papua New Guinea species, the Australian rainforest species and the Australian non-rainforest species.

Phenetic analyses, analysis of fixed differences, Hardy Weinberg equilibria analyses and phylogenetic analyses by Wagner trees of the electrophoretic data supported the recognition of

(1) all members of the ingroup as belonging to the genus *Corasoides*

(2) *C. australis* as a widespread species with a distribution across coastal Australia below 25 degrees South and inland up to 450 kilometres.

(3) eight new species of *Corasoides*. Four of these (represented by the code names Kuper, Largetown, Smalltown and Ambua) are rainforest inhabitants from Papua New Guinea. The other four are from Australia. One, represented here by SWWA, inhabits open woodland and scrub. The other three, represented here by the populations Windsor, Terania and Clyde, inhabit refugial rainforest habitat in eastern Australia.

These conclusions will be developed further in studies of the genus in preparation.

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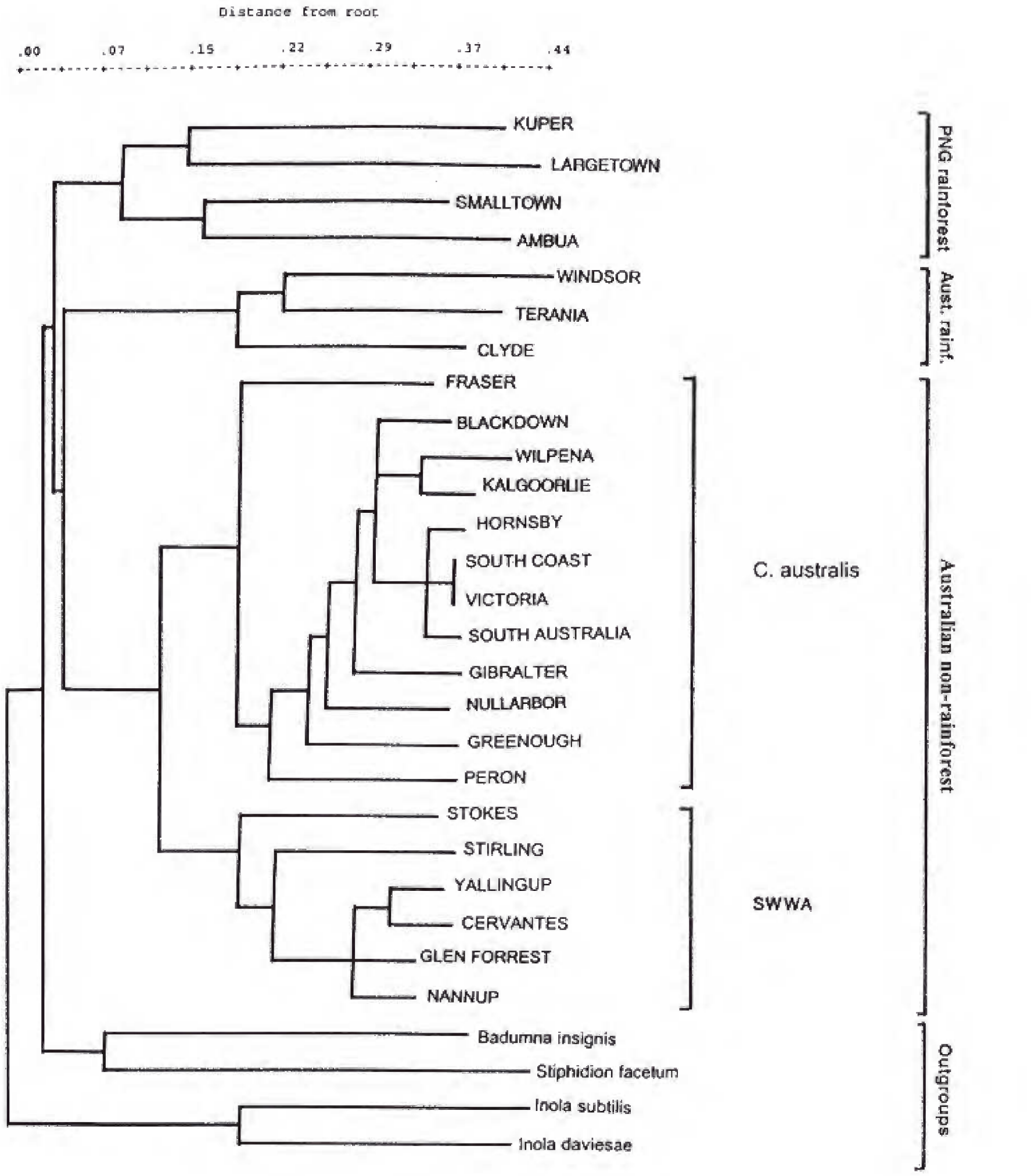

Fig. 5. Wagner tree of all populations of *Corasoides* sampled, *Badumna insignis*, *Stiphidion facetum*, *Inola subtilis* and *Inola daviesae* and rooted at the midpoint of the longest branch.

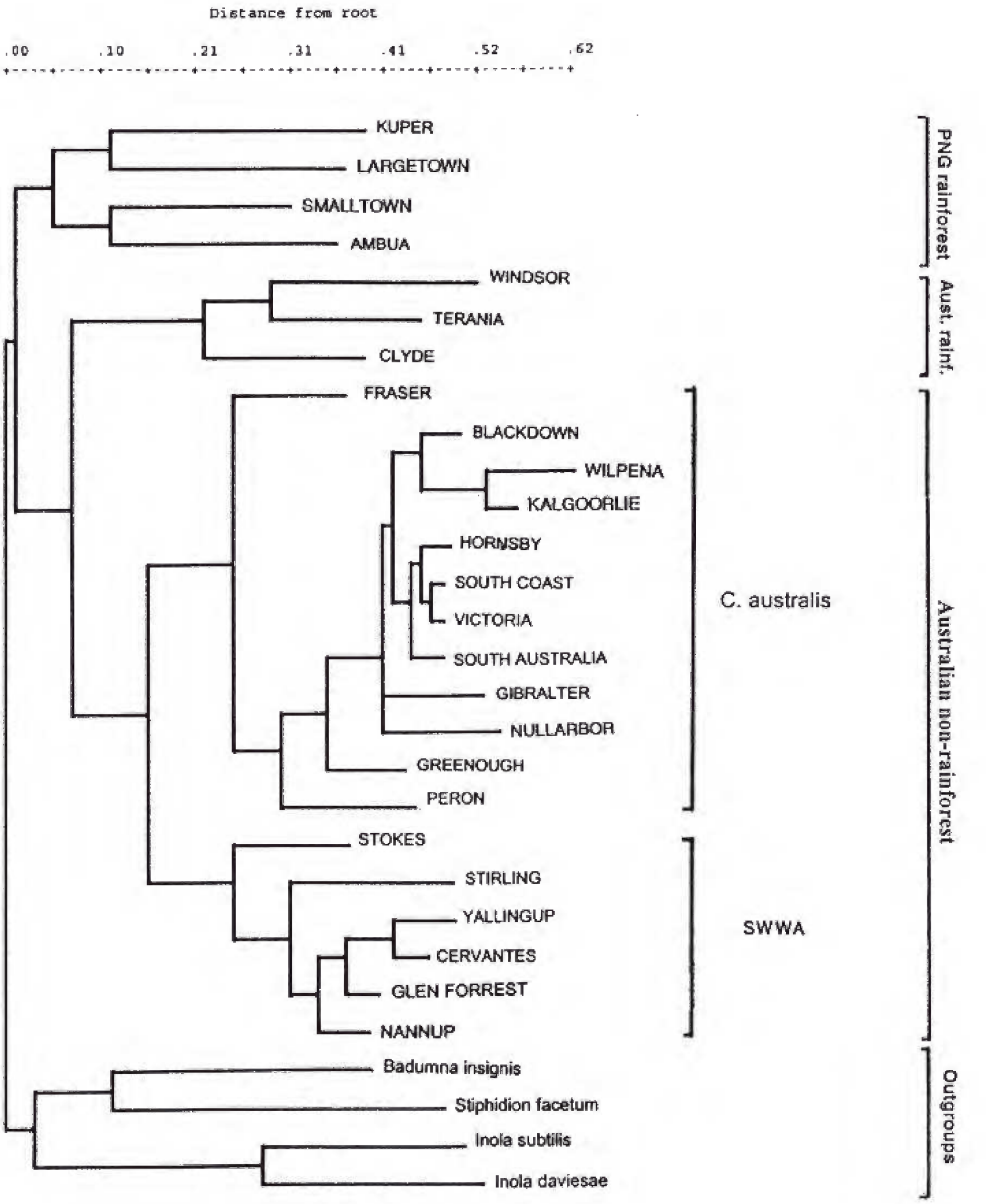

Fig. 6. Wagner tree of all populations of *Corasoides* sampled and rooted by outgroup using *Badumna insignis*, *Stiphidion facetum*, *Inola subtilis* and *Inola daviesae*.

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REFERENCES

Avise, J.C. (1975). Systematic value of electrophoretic data. *Systematic Biology* **23**: 465-481.

Baverstock, P.R., Watts, C.H.S. and Cole, S.R. (1977). Electrophoretic comparisons between the allopatric populations of five Australian Pseudomyine rodents (Muridae). *Australian Journal of Biological Sciences* **30**(5): 471-485.

Bruce, E.J. and Ayala, F.J. (1979). Phylogenetic relationships between man and the apes: electrophoretic evidence. *Evolution* **33**: 1040-1056.

Butler, L.S.G. (1929). Studies in Victorian spiders. *Proceedings of the Royal Society of Victoria* **42**: 42-52.

Colgan D.J. and Gray, M.R. (1992). The genetic structure of the *Badumna candida* group of species (Aranae, Amaurobioidae). *Bulletin of the British Arachnological Society* **9**: 86-94.

Colless, D.H. (1995). Relative symmetry of cladograms and phenograms: an experimental study. *Systematic Biology* **44**: 102-108.

Cook, L.M. (1971). Coefficients of Natural Selection. 207 pp. (Hutchinson: London).

Davies, V.T. (1982). *Inola* nov. gen., a web-building pisaurid (Araneae: Pisauridae) from northern Australia with descriptions of three species. *Memoirs of the Queensland Museum* **20**(3): 479-487.

Farris, J.S. (1970). Methods for computing Wagner trees. *Systematic Biology* **18**: 374-385.

Forster, R.R. and Wilton. C.L. (1973). The spiders of New Zealand Part IV. 309 pp. *Otago Museum Bulletin* **4**: 1-123.

Koch, L. (1872). Die Arachniden Australiens, nach der Natur beschrieben und abgebildet. Nurnberg: Bauer and Raspe. Vol. 1 Pp. 105-338. (330).

Lehtinen, P.T. (1967). Classification of the cribellate spiders and some allied families, with notes on the evolution of the suborder Araneomorpha. *Annales Zoologici Fennici* **4**:199-468.

Lewontin, R..C. (1974). The genetic basis of evolutionary change. 346 pp. (Columbia University Press).

Lubin, Y.D. and Crozier, R.H. (1985). Electrophoretic evidence for population differentiation in a social spider Achaearanea wau (Theriiidae). *Insectes Sociaux* **32**: 297-304.

Main, B.Y. (1976). Spiders. 296pp. (Collins: Sydney. Reprinted 1984).

Main, B.Y. (1982). Some geographic considerations of families of spiders occurring in New Guinea. Pp. 583-602. In Gressit, J.L. (Ed.), Monographiae Biologicae **42**(4). W.Junk: The Hague. 983 pp.

McDonald, J.F. (1983). The molecular basis of adaptation: a critical review of relevant ideas and observations. *Annual Review of Ecological Systematics* **14**: 77-102.

Nei, M. (1972). Genetic distance between populations. *The American Naturalist* **106**: 283-292.

Pennington, B.J. (1972). Enzyme genetics in taxonomy: diagnostic enzyme loci in the spider genus *Meta*. *Bulletin of the British Arachnological Society* 4: 377-391.

Quicke, D.L.J. (1993). Principles and techniques of contemporary taxonomy. 311 pp. (Chapman and Hall, London and Blackie Academic and Professional: Glasgow).

Richardson, B.J., Baverstock, P.R. and Adams, M. (1986). Allozyme electrophoresis. a handbook for animal systematics and population studies. 410 pp. (Academic Press, Sydney).

Rogers, J.S. (1972). Measures of genetic similarity and genetic distance. In:. Studies in genetics VII, University of Texas publication 7213: **145**-153.

Simon, E. (1902). Descriptions de quelque arachides nouveaux de la section de cribellates. *Bulletin de la Societe Entomologique de France* **1902**: 240-243.

Swofford, D.L. and Selander, R.B. (1981). BIOSYS–1: a FORTRAN program for the comprehensive analysis of electrophoretic data in population genetics and systematics. *Journal of Heredity* **72**: 281-183.

Tio, M. and Humphrey, M. (2010). Description of a new species of *Inola* Davies (Aranae: Pisauridae), the male of *I. subtilis* Davies and notes on their chromosomes. *Proceedings of the Linnean Society of New South Wales* **131**: 37-42.